



Neurogaming With Motion-Onset Visual Evoked Potentials (mVEPs): Adults Versus Teenagers

Beveridge, R., Wilson, S., Callaghan, M., & Coyle, D. (2019). Neurogaming With Motion-Onset Visual Evoked Potentials (mVEPs): Adults Versus Teenagers. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, 27(4), 572-581. [8664451]. <https://doi.org/10.1109/TNSRE.2019.2904260>

[Link to publication record in Ulster University Research Portal](#)

Published in:

IEEE Transactions on Neural Systems and Rehabilitation Engineering

Publication Status:

Published (in print/issue): 08/04/2019

DOI:

[10.1109/TNSRE.2019.2904260](https://doi.org/10.1109/TNSRE.2019.2904260)

Document Version

Author Accepted version

General rights

Copyright for the publications made accessible via Ulster University's Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Ulster University's institutional repository that provides access to Ulster's research outputs. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact pure-support@ulster.ac.uk.

Neurogaming with motion-onset visual evoked potentials (mVEPs): adults versus teenagers

Ryan Beveridge, Shane Wilson, Michael Callaghan, and Damien Coyle

Abstract— Motion-onset visually evoked potentials (mVEPs) are neural potentials that are time-locked to the onset of motion of evoking stimuli. Due to their visually elegant properties, mVEP stimuli may be suited to video game control given gaming's inherent demand on the users' visual attention and the requirement to process rapidly changing visual information. Here, we investigate mVEPs associated with 5 different stimuli to control the position of a car in a visually rich 3D racing game in a group of 15 BCI naïve teenagers and compared to 19 BCI naïve adults. Results from an additional 14 BCI experienced adults were compared to BCI naïve adults. Our results demonstrate that game control accuracy is related to the number of trials used to make a decision on the users' chosen button/stimulus (76%, 62% and 35% for 5, 3 and 1 trials, respectively) and information transfer rate (ITR) (13.4, 13.9 and 6.6 bits per minute (BPM)), although, even though accuracy decreases when using three compared to the commonly used five trial repetitions, ITR is maintained. A Kruskal-Wallis test suggests that BCI naïve adults do not outperform BCI naïve teenagers in the 3D racing game in the first and second laps ($p > 0.05$), but do outperform in the third lap ($p < 0.05$). A comparison between BCI naïve and BCI experienced adults indicates BCI experienced adults do not perform better than BCI naïve adults ($p > 0.05$).

Index Terms— brain-computer interface (BCI); motion-onset visually evoked potentials (mVEP); video game; electroencephalography (EEG); 3-dimensional (3D); neurogaming

I. INTRODUCTION

Visually evoked potential (VEP)-based brain-computer interfaces (BCIs) are a subset of BCIs which involve presenting visual stimuli in order to evoke a response in brain potentials measured using electroencephalography (EEG). Typically, flashing, flickering or moving visual stimuli are presented via computer screens/lighting panels to which the user attends visually. Each stimulus represents a command for the BCI system to process and execute.

P300 VEPs have been successful in BCI spelling applications [1][2] and neurogame control [3][4] and involve using stimuli which are flashed, either individually or in groups at specific times. When the users' gaze is focused on the intended target stimulus, a P300 response occurs i.e., a rare occurrence of the stimulus flash creates a positive peak in the EEG at around 300ms post-stimulus and often referred to as the "oddball paradigm" [5]. Steady-state VEPs (SSVEP) have been used in a number of BCI studies including BCI spellers [6], neurogames [7][8] and wheelchair/orthosis control [9][10]. Typically, a number of stimuli are presented, each flashing at a constant but fixed frequency. When the users' gaze is focused on the intended stimuli, the resulting EEG activity enters into a "steady-state" matching the fundamental frequency of the

flashing stimulus and its harmonics. Code-modulated VEPs (cVEP) involve flashing stimuli and have been used in BCI spelling applications [11][12], computer control [13] and control in virtual environments [14][15]. Typically, numerous stimuli are delineated on a screen/lighting board, each flashing at the same code-modulated flash rate but differentiated from each other using time-shifted code sequences.

Since the inception of BCIs, addressing the low communication rates available has been a major challenge. In a BCI, the communication rate between the user and computer is measured in bits per minute (BPM) and defined as information transfer rate (ITR). VEP-based BCIs offer the highest ITR compared to other neural potentials. Chen et al. [16] employed SSVEPs to control a spelling application resulting in the highest ITR of any BCI speller to date with communication rates of up to 319 BPM. Previously, cVEP-based BCIs spellers achieved ITR of up to 133 BPM [12]. Typically, P300 BCIs can achieve ITRs of around 43 BPM [17]. A disadvantage with 'flash'-based VEPs is that their reliance on flashing/flickering imagery can cause visual fatigue after long-term use [18][19]. Han et al [20] addressed the problem of visually fatiguing SSVEP stimuli with a steady-state motion visual evoked potential (SSMVEP) paradigm that used ring-shaped motion checkerboard patterns with oscillating expansion and contraction. In this visually less fatiguing and training free paradigm, 18 participants (10 BCI naïve) achieved an average accuracy of 94% and ITR 91.2BPM.

Motion-onset VEPs (mVEP) are an alternative to flash-based BCIs and evoked using motion-based stimuli. mVEPs have been used in BCI spelling applications [21], user interfaces [22] and neurogaming [23][24][25]. Typically, a mVEP stimulus comprises a rectangular white box with a black border with a total length of 1.24° and height of 0.76° . A red line of height 0.66° serves as the stimulus' salient object by appearing in the white box and beginning motion starting at the extreme right-hand side moving in one continuous motion to the left-hand side in 140 milliseconds (ms) and subsequently disappearing (Fig. 1). The perception of motion begins at the magnocellular layers of the primary visual cortex and extends to the medial temporal and medial superior temporal areas [26][27]. The mVEP response occurs following the sudden motion of a moving stimulus and is composed of three main peaks. The initial P100 positive peak occurs at approximately 100ms post-stimulus with its early phase (80-110ms) originating at the lateral extrastriate cortex and its later phase (110-140ms) emanating at the ventral occipitotemporal cortex [28]. The motion-specific N200 negative peak at approximately 160-200ms is the most prominent component and generated in the extrastriate temporo-occipital and parietal areas [29]. The positive P300 peak occurs at around 240-500ms post-stimulus and originates at the parietal up to central areas [22] whose amplitude can be

increased with more complex moving stimuli (Fig. 2). mVEPs offer a visually elegant BCI paradigm and reliable mVEP responses are elicited in the EEG even with low luminance values and contrasts as low as 20 cd/m² and 2%, respectively [29]. As mVEPs involve stimuli which are visually more elegant and subtle than other VEPs, they may be more suited to integration as a neurogame controller. Videogames typically have demanding visual stimuli/features that introduce continuous flickering like those used in VEPs, thus impacting the gameplay experience and causing visual fatigue.

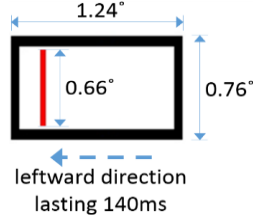


Fig. 1. Close-up of a single mVEP stimulus as used in this study. The red line inside the black box moves horizontally from right to left lasting for 140 milliseconds (ms).

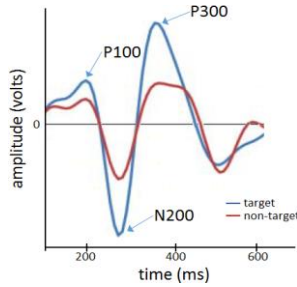


Fig. 2. A simulated mVEP response including P100, N200, P300 neural potentials. Due to the more pronounced peaks, there is a clear difference between the target (blue) and non-target (red) responses to moving imagery.

Marshall et al. [24] published the first mVEP-based paper relating to neurogaming and presented three video games from the action, puzzle, and sports genres. Game control was achieved using one of 5 available on-screen mVEP stimuli. Average offline accuracy across all participants for all games was >70% while online accuracy yielded accuracies of >60%. In a follow-up study [25] the approach was improved i.e., participants were trained and tested within the same environment, stimuli were delineated within a dedicated controller area and more control instances were added. All scenarios achieved average offline and online accuracies of >77%. Li et al. [30] exploited the N200 component of the mVEP response to control a robot. Six mVEP stimuli were used to control the robot's movements i.e., walk forward/backward, shift left/right and turn left/right. In an online evaluation, participants achieved average accuracies of 85% and 88% using 3 and 5 trials, respectively. In a second online evaluation, participants achieved 92% and 96% using 3 and 5 trials, respectively. In our previous work [23], we investigated the effects on mVEP classification performance with users subjected to different video game graphics, ranging from basic to state-of-the-art. Findings demonstrated the feasibility of using state-of-the-art commercial-grade graphics within mVEP-controlled neurogames. We also evaluated mVEP-based game control in a virtual-reality (VR) environment using an Oculus Rift [31] VR head-mounted display to display a mVEP-

based racing game with both basic and complex graphics [23]. Results showed that contemporary visual display technologies could be used in mVEP-based neurogaming without degrading mVEP detection accuracies, compared to a standard LCD monitor. In [32], we tested a group of fifteen BCI naïve teenagers who played an online 3D racing car game using mVEP stimuli to control a racing car. Using one of five stimuli, participants were asked to select the correct lane while the car travelled around a racing track. Across three laps, participants achieved an average online performance of 68% (11 BPM) with up to 95% accuracy (23 BPM).

Here, we evaluate further factors affecting mVEP detection accuracy and investigate if 19 of the 33 adults who were BCI naïve could perform better than the BCI naïve teenagers using mVEPs to play a 3D car racing game. While teenagers represent a smaller target audience for computer games than adults [33], understanding differences in performance was considered important for future neurogaming applications. Zhang et al. [34] used the commercially available EEG headset Emotiv Epoc [35] to study how effectively healthy children between the ages of 6 and 18 years could control a simple BCI using both VEP and motor imagery paradigms and report performance variances based on strategy, task and age. Here, as well as investigating the underrepresented children group in VEP BCI studies, a goal of the current study was to investigate a trade-off between accuracy of control and gameplay speed with mVEPs by varying the number of stimulus/trial repetitions used to make decisions related to game control. Variations in the speed of racing laps in the game resulted in slow, medium and fast laps. This paper addresses a number of limitations with current neurogames including; age group comparison; improvements in graphical quality; speed of control; reduced electrode montages; and VEP BCI calibration.

II. METHODOLOGY

A. Data acquisition setup

Fifteen healthy BCI naïve (nvBCI) teenagers (age range 13-16, 4 female) and 33 healthy adults (19 nvBCI and the remaining 14 had prior BCI experience (exBCI) age 18-40, 6 female) participated. Details of the teenagers study including results are available in [32]. Ethical approval was granted by the Ulster University Research Ethics Committee (UUREC). Written consent was provided by all participants. All participants had normal or corrected to normal vision. The teenagers completed an offline calibration run followed by three slow speed online racing laps within a single session. The adults also completed an offline calibration lap, followed by three each of the slow, medium and fast racing laps. The EEG setup involved g.Tec hardware [36] consisting of twelve g.LadyBird active EEG electrodes placed onto a g.GammaCap according to the international 10-20 system of electrode placement covering occipital areas Cz, TP7, CPz, TP8, P7, P3, Pz, P4, P8, O1, Oz, and O2 (Fig. 3). EEG was amplified with a g.BSamp signal amplifier and digitised at 250Hz with a National Instruments NI6390 analogue-to-digital data acquisition card [37]. The 3D racing game was created in the Unity 3D games engine [38]. A Matlab [39] session-based interface was used to store/process the raw EEG signals. As each of the visual stimuli were activated in the game, a unique stimulus identifier was sent over a user datagram protocol

(UDP) connection to Matlab. Once data processing completed, a number, 1-5, is relayed back to the game to perform a real-time action.

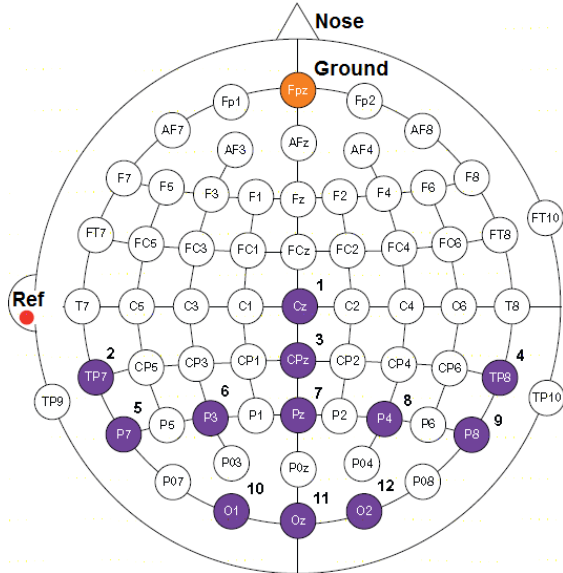


Fig. 3. The 12-channel EEG montage used for the study, covering the occipital areas (electrodes coloured in purple). The left ear was used as reference (ref) and the forehead electrode (Fpz - coloured in orange) used as ground.

B. BCI calibration

During the calibration run, responses of the user were not translated into in-game commands and instead stored for offline analysis and BCI calibration. The participants' task was to focus gaze on the target stimulus (Fig 1) out of the five available. The target stimulus on which the user should gaze was indicated by a red-coloured arrow cue placed directly above the stimuli (Fig. 4), whereas the four other (non-target) stimuli, indicated by a black coloured arrow were to be ignored. During the calibration run, the user viewed gaming scenes similar to those in the online game, with the exception of some online-specific gaming elements such as the car model, checkpoints, and on-road visual cues. In previous studies, it was shown that maintaining consistency between the calibration training and online visuals could have an impact on gaming with mVEPs, compared to using white screen background during the calibration runs [24][25]. During the calibration run, each of the five stimuli was a target 60 times yielding data from 300 trials (5 stimuli \times 60 activations). Individual trials lasted 1000ms and involved activation of each of the five stimuli in random order. Fig. 5 depicts the trial timing details of the calibration run.



Fig. 4. Participants' first-person view of the calibration run. The current target is stimulus 1 (left-hand side) which is currently active (red line is in motion) and indicated by a red-coloured arrow pointer located directly above the stimulus. All other stimuli are non-target, to be ignored by the participant and have black-coloured arrow pointers.

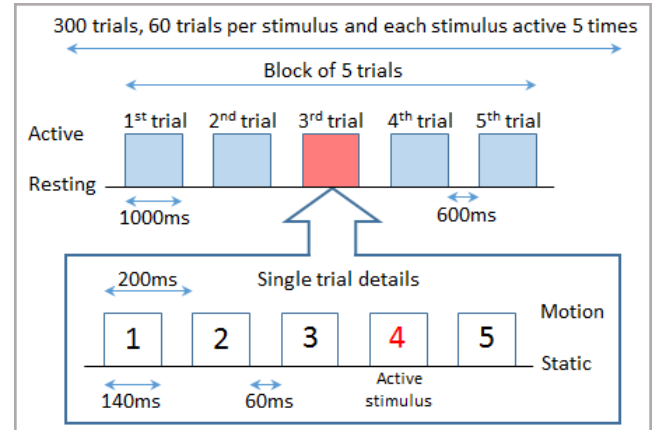


Fig. 5. Trial timing details of the calibration run. Each stimulus was active (in motion) for 140 milliseconds (ms) with a break between one stimulus and the next randomly selected stimulus lasting 60ms, yielding a stimulus onset asynchrony (SOA) of 200ms. There was a 600ms inter-trial interval (ITI).

C. Online game paradigm

A lap is defined as one complete circuit of the racing course from start to finish (Fig. 6).



Fig. 6. Aerial view of the racing course used in the game. Each of the 20 checkpoints are depicted by a red marker.

Typically, in mVEP-based BCI systems, the greater the number of trials used to detect the users' required stimulus, the more accurate the classification [30][40], but this can be at the expense of decreased control/communication/interaction speed. To investigate mVEP discrimination accuracy with 5, 3 and 1 trial(s), three different car speeds were used in the adult study: a slow speed lap that used 5 repetitions of the stimuli to provide

a game command per checkpoint, a medium speed lap with 3 trial repetitions and, a fast speed lap with a single repetition. Each adult participant completed nine laps – three each using 5, 3, and 1 trials for classification. As the lap speed changed, a different car was presented representing analogous achievement as in commercially available racing games [41][42]. Due to time restrictions on the teenage study, each teenage participant completed only three laps using 5 trials for classification [32]. Each lap of online gameplay contained twenty checkpoints and mVEP stimuli are presented twenty times, once for each checkpoint. The participant must choose the correct (indicated) lane out of five available. To accentuate individual control periods, stimuli are only presented and active when the player is making a lane choice and hidden while traversing the checkpoint. Visual cues in the form of five moving arrows were delineated onto the road surface ahead of the car and in the peripheral vision of the participant in advance of the checkpoint (Fig. 7). One green-coloured arrow depicts the target lane and four red-coloured arrows depict the non-target lanes. The participants' task was to quickly identify the green arrow prior to the presentation of the stimuli (each representing a game control, here defined as a 'button') and attend visually to the corresponding button whilst ignoring the remaining four non-target buttons. Participants were instructed to mentally count the number of times the target button was activated i.e., attend to its motion. Upon successfully identifying and subsequently choosing the button corresponding to the target lane, the car proceeds through the checkpoint at a fast speed taking one second of time while hitting a green-coloured arrow (Fig. 8), providing real-time feedback. If any of the four non-target lanes were chosen, the car progresses through the checkpoint at a slower speed taking two seconds of time while hitting the traffic cone corresponding to their chosen lane. The participant can complete each lap in the quickest possible time if all correct lanes are chosen. At the end of the lap, the completion time is shown to the participant. A player score was visible on the bottom right-hand side of the screen within the speedometer clock and updated at each checkpoint. 500 points were awarded for each correct lane chosen, 300 points were awarded if the participant chose either of the two lanes closest to the target and only 100 points were added if the participant chose any of the two lanes located farthest from the target lane. The maximum possible score was 10000 points (500 points \times 20 lanes). Fig. 9 depicts the games decision-making process.



Fig. 7. Players' third-person view of the on-road arrow cues ahead of the car to which the participant attends visually. All arrows flash which simulates visuals seen in commercially available racing games. The target lane (and

corresponding stimulus) on which the user should choose (gaze) is lane 3.



Fig. 8. User approaches each checkpoint containing one green arrow. If the correct lane has been chosen and classified, the user traverses the checkpoint and hits the green arrow in-game item, otherwise, a cone is hit.

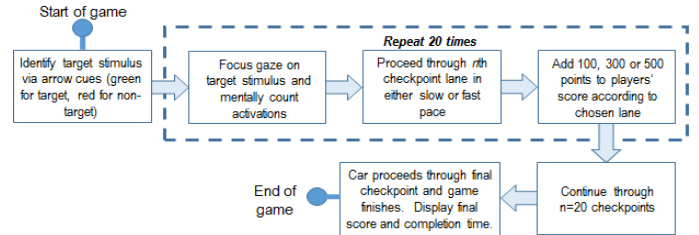


Fig. 9. Decision-making process of each lap from start to finish.

D. Data pre-processing and feature extraction

Data epochs were derived within individual trials and lasted for 1200ms beginning 200ms prior to the motion onset of the five stimuli and ran until all five stimuli were activated. Single trials were baseline corrected with respect to the mean voltage over the 200ms preceding individual trials. Data were digitally filtered using a low-pass Butterworth filter (order 5, with cut-off at 10Hz) and subsequently resampled at 20 samples per second. Features were extracted between the 100ms and 500ms epoch post-stimulus which normally contains the most reactive mVEP components e.g., P100, N200, and P300, yielding nine features per EEG channel. Data recorded in the calibration lap was used to train a classifier averaged on 5 trials, yielding twelve feature vectors per stimulus.

E. Offline mVEP classification – calibration data

Using the Biosig [43] toolbox, customised Matlab code was created for online/offline data analysis. To distinguish between target and non-target stimuli, all 300 trials of data collected in the calibration lap were used to train a linear discriminant analysis (LDA) classifier. A leave- p -out cross validation (LpOCV) procedure was applied (in this case, $p = 2$ where one target and one non-target were included in each test fold) for each of the twelve EEG channels which were subsequently ranked by accuracy. Features from the top three-ranked channels were concatenated to form a new feature vector containing 27 features. A further LpOCV was performed to assess performance with the best three channels. These offline results are reported as "train LpOCV 2-class". We upsampled non-target class data by repetition of target samples. This balances classes, ensures sufficient data for classifier training, negates randomness, maximises training accuracy and generalisation performance.

To classify individual symbols within a single trial test (i.e., 5-class discrimination), each feature vector associated with

each stimulus in a trial is classified as either target or non-target. The LDA classifier produces a distance value, D , reflecting the distance from the hyperplane separating target and non-target features ($D > 0$ depicts target features and $D < 0$ depicts non-target features). The classified stimulus is selected based on the vector with the maximum positive distance from the separating hyperplane (in some cases, non-target data produces a $D > 0$, however, the value of D is normally maximal among target stimulus). Single-trial results for 5-class discrimination are validated offline and reported as “train validation 5-class”.

Calibration data was subjected to the above classification procedure i.e., 5 trials were averaged to train the classifier which was then applied online for the slow, medium and, fast laps (5, 3 and 1 trial repetition(s), respectively).

F. Performance assessment - accuracy and information transfer rate

Online game control accuracy was assessed based on the ability of participants to select the correct stimuli from cues presented in the game. To account for time variations across different lap speeds, information transfer rate (ITR) was calculated [44][45]. For slow laps, each checkpoint requires five seconds of decision time to choose a lane, yielding a total of 100 seconds of concentration time (time spent controlling the BCI) per lap (i.e. 20 checkpoints \times 5s), for a medium lap, three seconds decision time was required to make a lane choice (20 checkpoints \times 3s decision time = 60 seconds) and a fast lap requires one second of decision time to make lane choices (20 checkpoints \times 1s). Taking into account that 5, 3 and 1 second(s) of time is required per checkpoint for the slow, medium and fast laps, respectively, 12, 20 and 60 commands per minute (CPM) are required for three lap speeds. ITR, reported in bits per minute (BPM) is calculated in equation 1, where N is the number of classes and P is the probability of correct classification.

$$BPM = (\log_2(N) + P \log_2(P) + (1 - P) \log_2(\frac{1-P}{N-1})) \times CPM \quad (1)$$

To evaluate significant differences between groups we used a Kruskal-Wallis test, a rank-based non-parametric test to determine if there are statistically significant differences between 2 or more groups of an independent variable on a continuous or ordinal dependent variable. This test can be easily applied to imbalanced group results.

III. RESULTS

A. nvBCI teenage vs nvBCI adult participants

The calibration and slow lap data from the nvBCI teenagers and the nvBCI adults were compared. Adults achieved higher average accuracies in both the train LpOCV 2-class and train validation 5-class offline analysis tests (Table I). The offline performance differences between the adults and teenagers were not statistically significant for the LpOCV 2-class ($p = 0.1358$) and train validation 5-class comparisons ($p = 0.1139$). In terms of online performance, the adults achieved higher accuracies than teenagers in all laps (Table II). For each lap, the differences of adults and teenagers were compared. Although accuracy of adults is higher than teenager across all laps the differences were found to be insignificant in lap 1 ($p = 0.3913$) and lap 2 (p

$= 0.4130$), whilst for lap 3 the differences between adults and teenagers were significant ($p = 0.0414$).

TABLE I
AVERAGE RESULTS OF THE OFFLINE CALIBRATION LAP BETWEEN BCI NAÏVE TEENAGERS AND BCI NAÏVE ADULTS. LEAVE P OUT CROSS VALIDATION (LPOCV) 2-CLASS AND TRAIN VALIDATION 5-CLASS.

Offline Analysis	LpOCV 2-class		Validation 5-class	
	Teenagers	Adults	Teenagers	Adults
Mean Across all Participants	85.2	88.4	80.9	85.8
Difference	$p = 0.1358$		$p = 0.1139$	

TABLE II
AVERAGE ACCURACY AND INFORMATION TRANSFER RATE (ITR) OF THE ONLINE LAPS (5 TRIALS) BCI NAÏVE TEENAGERS VS. BCI NAÏVE ADULTS.

Online Analysis	Lap 1		Lap 2		Lap 3	
	Teenagers	Adults	Teenagers	Adults	Teenagers	Adults
Accuracy (%)	71.7	76.3	67.0	71.8	65.4	78.2
ITR (BPM)	12.0	14.3	10.3	12.3	9.9	14.8
Difference	$p = 0.3913$		$p = 0.4130$		$p = 0.0414$	

B. BCI naïve vs. BCI experienced adults

The adult cohort consists a mixture of exBCI and nvBCI participants. We calculated the accuracy and ITR of the online laps to compare the nvBCI and exBCI adults (Tables III, IV and V). Some tests showed that nvBCI adults achieved higher accuracies than exBCI adults and vice-versa, but in no tests were significant differences found.

TABLE III
AVERAGE ACCURACY (%) AND INFORMATION TRANSFER RATE (ITR) IN BITS PER MINUTE (BPM) - ONLINE LAPS 5 TRIALS BCI NAÏVE VS. BCI EXPERIENCED ADULTS.

Online Analysis (5 trials)	Lap 1		Lap 2		Lap 3	
	Naïve	Experienced	Naïve	Experienced	Naïve	Experienced
Accuracy (%)	76.3	79.3	71.8	77.5	78.2	72.9
ITR (BPM)	14.3	14.7	12.3	14.2	14.8	12.5
Difference	$p = 0.9852$		$p = 0.4736$		$p = 0.4302$	

TABLE IV
AVERAGE ACCURACY (%) AND INFORMATION TRANSFER RATE (ITR) IN BITS PER MINUTE (BPM) - ONLINE LAPS 3 TRIALS BCI NAÏVE VS. BCI EXPERIENCED ADULTS.

Online Analysis (3 trials)	Lap 1		Lap 2		Lap 3	
	Naïve	Experienced	Naïve	Experienced	Naïve	Experienced
Accuracy (%)	60.0	61.8	65.0	64.6	63.4	63.6
ITR (BPM)	12.6	13.9	15.4	14.4	15.0	14.5
Difference	$p = 0.7693$		$p = 0.7412$		$p = 0.9127$	

TABLE V
AVERAGE ACCURACY (%) AND INFORMATION TRANSFER RATE (ITR) IN BITS PER MINUTE (BPM) - ONLINE LAPS 1 TRIAL BCI NAÏVE VS. BCI EXPERIENCED ADULTS.

Online Analysis (1 trial)	Lap 1		Lap 2		Lap 3	
	Naïve	Experienced	Naïve	Experienced	Naïve	Experienced
Accuracy (%)	38.95	32.5	34.2	32.5	35.8	31.8
ITR (BPM)	11.0	6.3	7.7	6.2	9.6	5.8
Difference	$p = 0.1888$		$p = 0.7398$		$p = 0.5333$	

C. EEG channel selection

The three highest-ranked EEG channels for both nvBCI and exBCI adults were P7, O1, and P3 (Fig. 10, left), demonstrating the most active EEG channels located on the left hemisphere. The three highest-ranked EEG electrodes across nvBCI teenagers were Cz, P7, and O1, demonstrating activity around the left up to central areas with some bilateral activity i.e., electrodes O2 and P8 providing features (Fig. 10, right). Data recorded from the calibration level was used to conduct an analysis of all twelve electrodes providing an indication of the

potential accuracies achievable if an optimal number of electrodes were used for classification (Fig. 11). Considering the nvBCI adults, the use of the two highest ranked electrodes provides 79.5% accuracy and using the three highest ranked electrodes, as used in the study, provided an average accuracy of 85%. Adding any more than nine of the highest ranked electrodes for the nvBCI adults did not increase the accuracy significantly. For the exBCI adults, the use of the two highest ranked electrodes provides 72.6% accuracy and using the three highest ranked electrodes provided an average accuracy of 84.3%. Adding any more than eight of the highest ranked electrodes for the nvBCI adults did not increase the accuracy significantly. For the nvBCI teenagers, a minimum of three electrodes were required to achieve >70% accuracy (76.2%) and by adding any more than eight of the highest ranked electrodes, accuracy did not increase significantly. Considering the 5-class analysis, 70% accuracy is 50% above the chance level of 20% in this 5-class paradigm. To achieve this accuracy, both adults and teenagers, required just three electrodes.

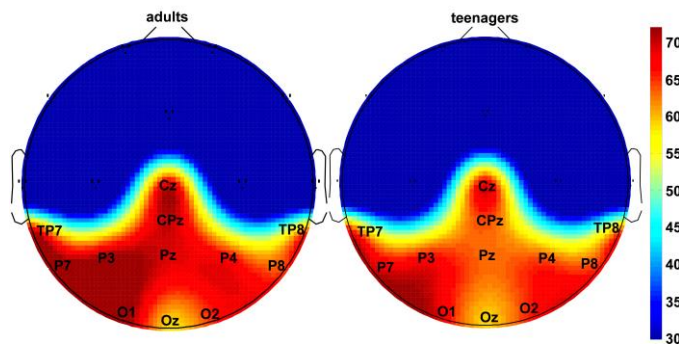


Fig. 10. Topographic representation of the three highest ranked electrodes across all adults (left) and teenage (right) participants. Colourbar depicts accuracy (%).

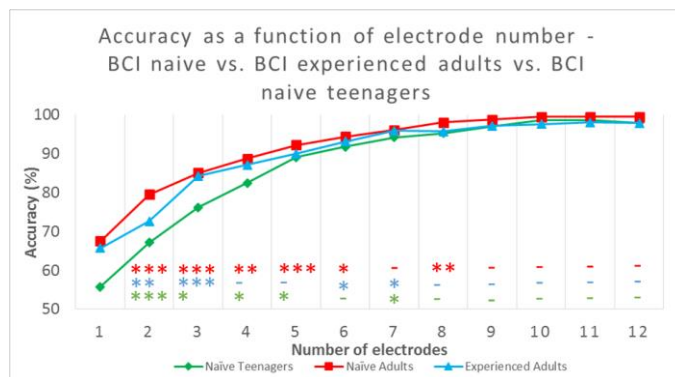


Fig. 11. Accuracy as a function of electrode numbers nvBCI vs. exBCI adults vs. nvBCI teenagers. Differences annotated in asterisks' are colour-coded according to individual groups and highlighted among groups at each electrode number. Key: *** = $p < 0.001$; ** = $p < 0.005$; * = $p < 0.05$; - = not statistically significant.

Comparing all adults to the teenagers, statistically significant differences ($p < 0.05$) were found between the two groups for electrodes TP7, CPz, P3, Pz, and P4 (Fig. 12).

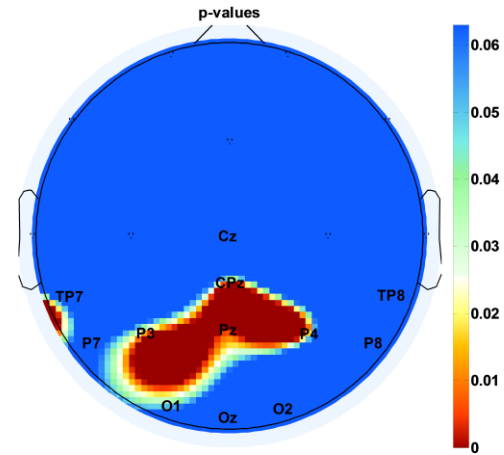


Fig. 12. Topographic plot depicting statistically significant differences in electrodes adults vs. teenagers. Electrodes TP7, CPz, P3, Pz, and P4 are significantly different ($p < 0.05$) between the 2 groups. Colourbar depicts p -values.

D. mVEP features

Considering the highest-ranking EEG channel in each participant group (i.e., Cz for the teenagers and P7 for the adults), mVEP features were analysed. The mVEP components were averaged across participants in each group. For all groups, there is a clear difference in P100, N200 and P300 amplitude between the average for target and non-target stimuli (figs. 13, 14 and 15).

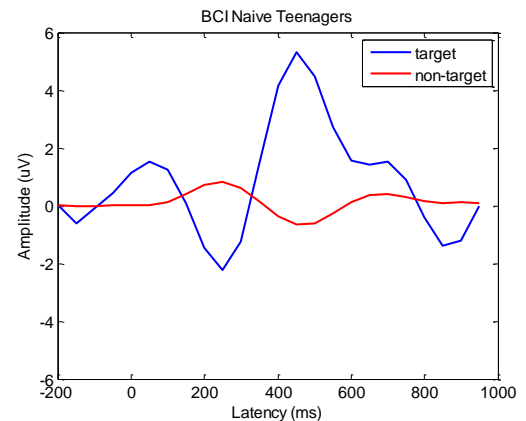


Fig. 13. Average mVEP features for channel Cz across all trials for the BCI naïve teenagers. Target (blue line) vs. non-target stimuli (red line).

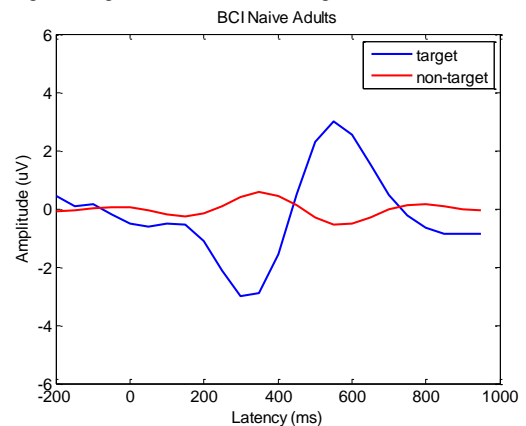


Fig. 14. Average mVEP features for channel P7 across all trials for the BCI naïve adults. Target (blue line) vs. non-target stimuli (red line).

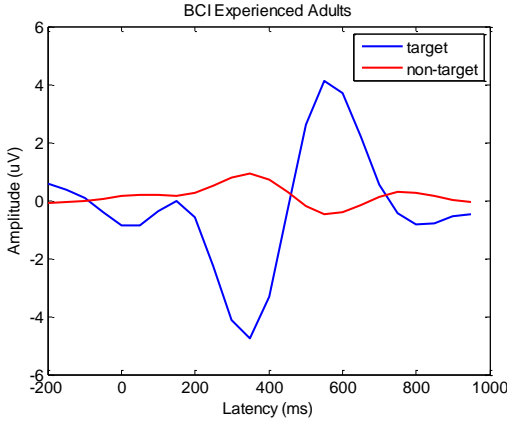


Fig. 15. Average mVEP features for channel P7 across all trials for the BCI experienced adults. Target (blue line) vs. non-target stimuli (red line).

We compared the latencies and amplitudes of the most reactive mVEP feature (N200) to assess differences across the different groups (Table VI). Differences in N200 latency between the nvBCI teenage and nvBCI adults show that the N200 latency for the adults were significantly later ($p=0.0062$). N200 amplitude differences between the nvBCI teenagers and nvBCI adults show that adults have a higher amplitude than the teenagers for all buttons except for button 2 ($p=0.2506$).

Differences in N200 latency between the nvBCI adults and exBCI adults show that the N200 latency for the exBCI adults were significantly later for buttons 1, 2 and 4 and the same for buttons 3 and 5 ($p=0.0495$). N200 amplitude differences between the nvBCI and exBCI adults show that exBCI adults have a higher amplitude than the nvBCI adults for all buttons ($p=0.009$). Figure 16 depicts the features obtained from the target vs. all other non-target buttons averaged across all participants.

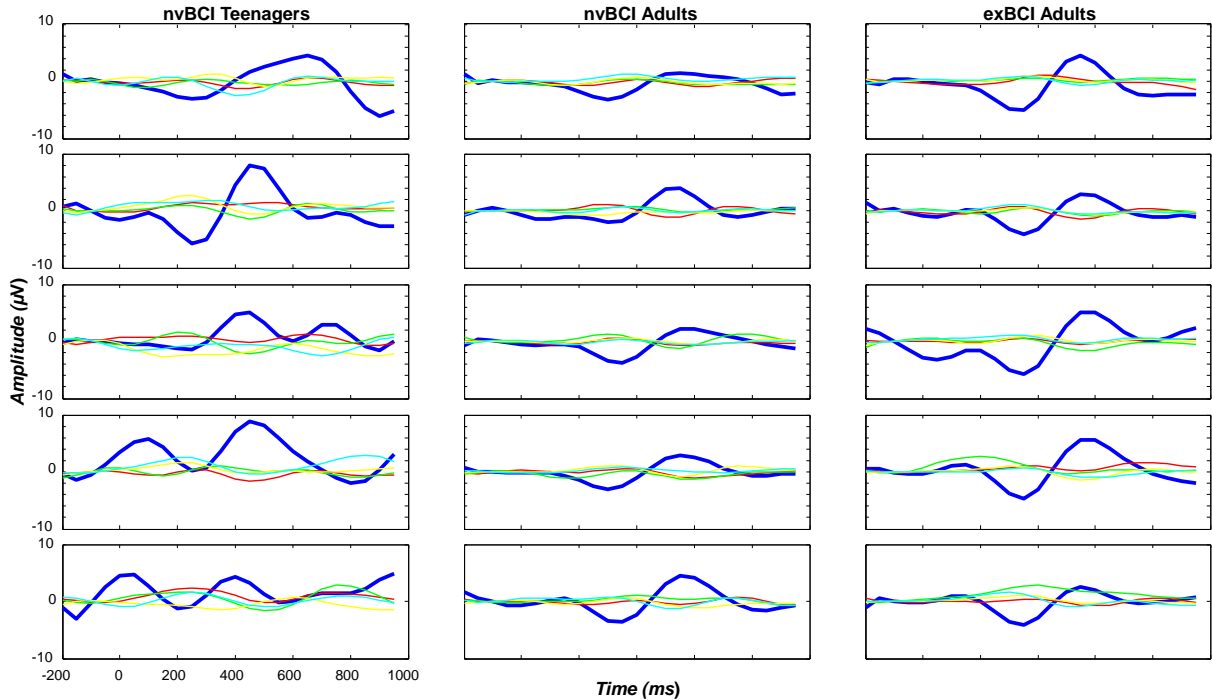


Fig. 16. Averaged mVEP features of all 5 target vs. the non-target buttons (stimuli) for all participant groups (buttons 1 to 5 are depicted from top to bottom, respectively). The y axis is the amplitude in microvolts (μV) and the x axis is the latency in milliseconds (ms). In each plot, the thick blue line depicts the target button and all other thinner coloured lines are the non-target buttons.

TABLE VI
AVERAGE N200 LATENCIES AND AMPLITUDES OF ALL PARTICIPANT GROUPS.
TABLE DEPICTS AVERAGED N200 mVEP RESPONSE ACROSS ALL FIVE
BUTTONS.

	nvBCI teenagers		nvBCI adults		exBCI adults	
target	latency (μV)	amplitude (ms)	latency (μV)	amplitude (ms)	latency (μV)	amplitude (ms)
button 1	250	-3.113	300	-3.272	350	-5.069
button 2	250	-5.818	300	-2.045	350	-4.12
button 3	250	-1.394	350	-3.719	350	-5.803
button 4	250	0.187	300	-3.02	350	-4.601
button 5	200	-1.344	350	-3.679	350	-4.162

IV. DISCUSSION

A. BCI naïve adults vs BCI naïve teenagers

Offline 2-class and 5-class results suggest the performance of the nvBCI adults do not significantly differ to the nvBCI teenagers. Online results showed that nvBCI adults achieved higher accuracies and ITR than the nvBCI teenagers in all laps, but this accuracy only differed significantly in lap 3. Accuracy is tipped in favour of the nvBCI adults and the difference between nvBCI adults and nvBCI teenagers widens as the session progresses across the three laps which does suggest that adults outperform teenagers, however, further trials are necessary to obtain conclusive evidence to support this assertion.

Analysis of the mVEP features in figs. 13 to 15 has shown that the latencies of all mVEP components are later in all adults than nvBCI teenagers, while P300 amplitudes were higher for the teenagers. However, amplitude of the N200 component were higher for both adult groups. It is commonly reported in the literature that the N200 component is the most distinct response to motion onset [29][46][21], which could explain the greater classification accuracies achieved by the adults. Interestingly, amplitude of the N200 component is lower for the nvBCI adults than the exBCI adults, but the nvBCI adults obtained higher classification accuracies in more online laps

than the exBCI adults. This may suggest that experience may not have an impact on mVEP classification accuracies, strengthening the case that lengthy training periods are not necessary in this paradigm.

The discrepancy in the sample size between the nvBCI adult and nvBCI teenage cohorts may have compounded results. Kuba [47] suggests that amplitudes of mVEPs did not display any significant changes for between age groups 6-18 years and 19-60 years. Conversely, our results show differences in amplitude for the teenagers and adults, which may be due to a difference in paradigm i.e., in [47] mVEP stimuli were displayed within a rudimentary interface, whereas in our study, stimuli were displayed within a dynamic gaming environment.

A previous study by Stelt et al. [48] involving 80 participants from the ages of 7-24 years investigated a visual selection task requiring the detection of the occurrence of targets among non-target images. Results showed that, among other event-related potential (ERP) components, reduced N200 latencies were observed for the adults in the 19-24 years age range than all other (younger) age groups tested. Subsequently, a decrease in error rates in the task as a function of age is reported. The finding that teenagers and children underperform in visual attention during target detection and have less reactive ERP components may explain the inferior classification accuracies achieved by teenagers in this study. The teenagers' performance declined as the session progressed, which suggests that their attention may have waned over time more dramatically than the adults. This finding is supported by research that suggests that adults visual processing and attention is more developed than children and thus adults are more likely to perform better at visual processing tasks and retain attention in prolonged assessments [49][50].

Our results suggest that studies and applications should target users of different age groups to test the viability of mVEP-controlled neurogames for a wide range of users, therefore, we recommend that BCI studies should report performance of different age groups, particularly in ERP-based BCI studies.

B. Increased ITR and faster gameplay – adults

Accuracy increases as a function of the number of trials used for classification [30][40]. This is expected as the features derived from fewer trials are less separable i.e., increasing the number of trials from which to derive features can sharpen the ERP response and reduce noise. Although accuracy is reduced using fewer trials, our results show no significant difference in ITR when using 3 compared to 5 trials for the adult groups, suggesting the feasibility of using a lower number of just 3 trials for classification in mVEP neurogaming. Therefore, there is a good trade-off between accuracy and latency to enable a faster decision-making process, faster gameplay and more challenges per unit time for the player. Performance reduced significantly when 1 trial was used, suggesting the use of 3 trials may be optimal for a speed/accuracy trade-off in mVEP-controlled neurogaming.

A different trend is observed for adult participants S4, S15, S17, and S28, where they have shown greater performance using 3 compared to 5 trials indicating that attention span required for 5 trials may negatively impact performance.

C. Ranking players - adults

We ranked participants based on accuracy separately for each lap speed and then averaged ranks. Ranking varied depending on the lap speed i.e., no individual participant dominated performance across all lap speeds e.g., S3 (aged 21) (nvBCI) ranked 1st in the slow and medium speed laps but 12th in the fast speed lap and therefore ranked 4th on average overall. S9 (aged 30) (nvBCI) ranked 5th and 3rd on the slow and medium speed laps, but 1st on the fast lap, subsequently ranking 1st overall.

These results suggest that each player in mVEP-based neurogaming could outperform others using different strategies and/or if they have a naturally strong single trial mVEP response, therefore, they have a significant advantage to improve their overall performance. This could make for interesting competitiveness, skills, and strategies in mVEP-controlled neurogaming. Further work could explore learning effects to determine if mVEP characteristics can be improved, if less trials can be used as the participant gains experience or if there are habituation effects that result in decreased performance. Questions that centre around skill development in mVEP-based neurogaming remain to be addressed, whereas it is well known that players/participants can enhance performance through motor learning during gameplay with motor imagery to modulate sensorimotor rhythms [51][52].

D. Spatial parameters and electrode requirements for mVEPs

Corroborating our previous findings, cortical activity using left-moving mVEP stimuli dominated the left visual hemisphere in adults. For the teenagers, the left hemisphere up to central areas were most active with some bilateral activity. This supports the occurrence of motion processing around the middle temporal (MT) and medial superior temporal (MST) areas [27]. Our analysis (fig. 11), shows the use of just 2 electrodes enabled the adults to gain >70% accuracy, whereas, the teenagers required three electrodes to gain >70% accuracy, suggesting that age-related montages for mVEPs should be studied in the future. Three electrodes in the adults and teenagers here are sufficient for mVEP control well above chance level. A reduced EEG electrode montage represents an important finding for the future of neurogaming in that it offers a convenient, inexpensive and less obtrusive EEG hardware setup. Cross analysis of the best three ranking electrodes from our previous studies (data gathered from 82 participants) exemplifies that the most active three electrodes using this mVEP paradigm were P7, O1 and P3.

V. CONCLUSION

A potential issue with VEP-based BCIs is the onset of visual fatigue, particularly after long-term use [18][19]. An inherent limitation with BCIs is the latency involved in detecting a reliable response from EEG. Previous neurogaming studies have employed rudimentary gameplay and graphical fidelity [53][54][55]. Here, we have employed high-fidelity graphics and gameplay scenarios akin to commercially available video games within a visually elegant mVEP-based controller. Our findings suggest that mVEP-based neurogaming is feasible for both adults and teenagers. In our analysis, nvBCI and exBCI adults achieved higher classification accuracies compared to nvBCI teenagers, but the difference between adults and

teenager is significant only in lap 3. Although accuracy is reduced when adults play the medium (3 trials) compared to the slow speed laps (5 trials), ITR is not significantly reduced. The findings have implications for BCI control strategies involving mVEPs in neurogaming i.e. gameplay quality, speed of control and calibration for target audiences.

A commonly studied application area suitable for BCI control and perhaps one of the most helpful is to provide movement independent technology interaction and communication devices for the physically impaired [52]. BCI controlled assistive devices are also commonly studied in the field [56]. A next step in this research is to compare the performance of those with physical disabilities and explore other target benefits of mVEP-based paradigms for the physically impaired.

REFERENCES

- [1] L. Farwell and E. Donchin, "Talking off the top of your head: toward a mental prosthesis utilizing event-related brain potentials.," *Electroencephalogr. Clin. Neurophysiol.*, vol. 70, no. 6, pp. 510–23, Dec. 1988.
- [2] J. Jin, E. W. Sellers, S. Zhou, and Y. Zhang, "A P300 Brain – Computer Interface Based on a Modification of the Mismatch Negativity Paradigm," *Int. J. Neural Syst.*, vol. 25, no. 3, pp. 1–12, 2015.
- [3] A. Finke, A. Lenhardt, and H. Ritter, "The MindGame: a P300-based brain-computer interface game," *Neural Netw.*, vol. 22, no. 9, pp. 1329–33, Nov. 2009.
- [4] G. Pires, M. Torres, N. Casaleiro, U. Nunes, and M. Castelo-Branco, "Playing Tetris with non-invasive BCI," in *2011 IEEE 1st International Conference on Serious Games and Applications for Health (SeGAH)*, 2011, pp. 1–6.
- [5] W. S. Pritchard, "Psychophysiology of P300.," *Psychological Bulletin*, vol. 89, no. 3. American Psychological Association, US, pp. 506–540, 1981.
- [6] E. Yin, Z. Zhou, J. Jiang, F. Chen, Y. Liu, and D. Hu, "A speedy Hybrid BCI spelling approach combining P300 and SSVEP.," *IEEE Trans. Biomed. Eng.*, vol. 61, no. 2, pp. 473–83, Feb. 2014.
- [7] P. Martinez, H. Bakardjian, and A. Cichocki, "Fully online multicommand brain-computer interface with visual neurofeedback using SSVEP paradigm.," *Comput. Intell. Neurosci.*, vol. 2007, pp. 1–9, Jan. 2007.
- [8] E. C. Lalor, S. P. Kelly, C. Finucane, R. Burke, R. Smith, R. B. Reilly, and G. McDarby, "Steady-State VEP-Based Brain-Computer Interface Control in an Immersive 3D Gaming Environment," *EURASIP J. Adv. Signal Process.*, vol. 2005, no. 19, pp. 3156–3164, 2005.
- [9] Y. Punsawad and Y. Wongsawat, "Hybrid SSVEP-motion visual stimulus based BCI system for intelligent wheelchair.," *Conf. Proc. IEEE Eng. Med. Biol. Soc.*, vol. 2013, pp. 7416–9, Jul. 2013.
- [10] A. H. Do, P. T. Wang, C. E. King, S. N. Chun, and Z. Nenadic, "Brain-Computer Interface Controlled Robotic Gait Orthosis," *J. Neuroeng. Rehabil.*, vol. 10, no. 111, pp. 1–9, 2013.
- [11] G. Bin, X. Gao, Y. Wang, Y. Li, B. Hong, and S. Gao, "A high-speed BCI based on code modulation VEP," *J. Neural Eng.*, vol. 8, no. 1, pp. 1–5, 2011.
- [12] M. Spuler, W. Rosenstiel, and M. Bogdan, "Online Adaptation of a c-VEP Brain-Computer Interface (BCI) Based on Error-Related Potentials and Unsupervised Learning," *PLoS One*, vol. 7, no. 12, 2012.
- [13] M. Spuler, "A Brain-Computer Interface (BCI) system to use arbitrary Windows applications by directly controlling mouse and keyboard," *Proc. Annu. Int. Conf. IEEE Eng. Med. Biol. Soc. EMBS*, vol. 2015–Novem, pp. 1087–1090, 2015.
- [14] H. Riechmann, A. Finke, and H. Ritter, "Using a cVEP-Based Brain-Computer Interface to Control a Virtual Agent," *IEEE Trans. Neural Syst. Rehabil. Eng.*, vol. 24, no. 6, pp. 692–699, 2016.
- [15] C. Kapeller, C. Hintermuller, M. Abu-Alqumsan, R. Pruckl, a. Peer, and C. Guger, "A BCI using VEP for continuous control of a mobile robot," *Proc. Annu. Int. Conf. IEEE Eng. Med. Biol. Soc. EMBS*, pp. 5254–5257, 2013.
- [16] X. Chen, Y. Wang, M. Nakanishi, X. Gao, T. Jung, and S. Gao, "High-speed spelling with a noninvasive brain – computer interface," *Proceedings Natl. Acad. Sci. United States Am.*, vol. 112, no. 44, pp. 1–11, 2015.
- [17] A. Turnip, S. S. Hutagalung, J. Pardede, and D. Soetraprawata, "P300 Detection Using a Multilayer Neural Network Classifier Based on Adaptive Feature Extraction," *Int. J. Brain Cogn. Sci.*, vol. 2, no. 5, pp. 63–75, 2013.
- [18] M. A. S. Boksem, T. F. Meijman, and M. M. Lorist, "Effects of mental fatigue on attention : An ERP study," *Cogn. Brain Res.*, vol. 25, pp. 107–116, 2005.
- [19] G. Faber, N. M. Maurits, and M. M. Lorist, "Mental Fatigue Affects Visual Selective Attention," *PLoS One*, vol. 7, no. 10, pp. 1–10, 2012.
- [20] C. Han, G. Xu, J. Xie, C. Chen, and S. Zhang, "Highly Interactive Brain – Computer Interface Based on Flicker-Free Steady-State Motion Visual Evoked Potential," *Sci. Rep.*, vol. 8, no. 1, pp. 1–13, 2018.
- [21] B. Hong, F. Guo, T. Liu, X. Gao, and S. Gao, "N200-speller using motion-onset visual response.," *Clin. Neurophysiol.*, vol. 120, no. 9, pp. 1658–66, Sep. 2009.
- [22] F. Guo, B. Hong, X. Gao, and S. Gao, "A brain-computer interface using motion-onset visual evoked potential.," *J. Neural Eng.*, vol. 5, no. 4, pp. 477–85, Dec. 2008.
- [23] R. Beveridge, S. Wilson, and D. Coyle, "3D graphics, virtual reality, and motion-onset visual evoked potentials in neurogaming.," *Prog. Brain Res.*, vol. 228, pp. 329–353, 2016.
- [24] D. Marshall, S. Wilson, and D. Coyle, "Motion-Onset Visual Evoked Potentials for Gaming," in *8th International Conference on Computer Games, Multimedia and Allied Technology*, 2015, pp. 155–164.
- [25] D. Marshall, R. Beveridge, S. Wilson, and D. Coyle, "Interacting with Multiple Game Genres using Motion Onset Visual Evoked Potentials," in *The 20th International Conference on Computer Games*, 2015, pp. 18–27.
- [26] W. T. Newsome, R. H. Wurtz, and H. Komatsu, "Relation of Cortical Areas MT and MST to Pursuit Eye Movements. II. Differentiation of Retinal from Extraretinal Inputs," *J. Neurophysiol.*, vol. 60, no. 2, pp. 604–620, 1988.
- [27] U. J. Ilg, "The role of areas MT and MST in coding of visual motion underlying the execution of smooth pursuit," *Vision Res.*, vol. 48, no. 20, pp. 2062–2069, 2008.
- [28] F. Di Russo, A. Martínez, M. I. Sereno, S. Pitzalis, and S. a. Hillyard, "Cortical sources of the early components of the visual evoked potential," *Hum. Brain Mapp.*, vol. 15, no. 2, pp. 95–111, 2002.
- [29] M. Kuba and Z. Kubova, "Visual Evoked Potentials Specific for Motion onset," *Doc. Ophthalmol.*, vol. 80, pp. 83–89, 1992.
- [30] W. Li, M. Li, and J. Zhao, "Control of humanoid robot via motion-onset visual evoked potentials," *Front. Syst. Neurosci.*, vol. 8, no. January, pp. 1–11, 2015.
- [31] Oculus, "Oculus Rift," 2016. [Online]. Available: <http://www.oculus.com/>. [Accessed: 05-Aug-2016].
- [32] R. Beveridge, S. Wilson, and D. Coyle, "Can teenagers control a 3D racing game using motion-onset visual evoked potentials?," *Brain-Computer Interfaces*, vol. 2621, no. January, pp. 1–12, 2017.
- [33] ESA, "Essential Facts About the Computer and Video Game Industry," 2016.
- [34] J. Zhang, Z. Jadavji, E. Zewdie, and A. Kirton, "Evaluating If Children Can Use Simple Brain Computer Interfaces," *Front. Hum. Neurosci.*, vol. 13, no. February, pp. 1–7, 2019.
- [35] EMOTIV, "EPOC+," 2016. [Online]. Available: <https://www.emotiv.com/epoc/>. [Accessed: 15-Sep-2016].
- [36] Guger Technologies, "g.tec Medical Engineering," 2016. [Online]. Available: <http://www.gtec.at/>. [Accessed: 05-Aug-2016].
- [37] NI, "National Instruments," 2016. [Online]. Available: <http://www.ni.com/en-gb.html>. [Accessed: 13-Oct-2016].
- [38] Unity Technologies, "Unity 3D," 2016. [Online]. Available: <http://unity3d.com/>. [Accessed: 05-Aug-2016].
- [39] "Matlab Session based Interface," *Matlab*, 2017. [Online]. Available: https://uk.mathworks.com/help/daq/examples/getting-started-with-session-based-interface-using-ni-devices.html?s_tid=gn_loc_drop. [Accessed: 22-Dec-2017].
- [40] R. Zhang, P. Xu, R. Chen, T. Ma, X. Lv, F. Li, P. Li, T. Liu, and D.

- Yao, "An adaptive motion-onset VEP-based brain-computer interface," *IEEE Trans. Auton. Ment. Dev.*, vol. 7, no. 4, pp. 1–8, 2015.
- [41] Sony Computer Entertainment, "Gran Turismo 6," 2013. [Online]. Available: <http://www.gran-turismo.com/gb/products/gt6/>.
- [42] Microsoft, "Forza Motorsport," 2017. [Online]. Available: <https://www.forzamotorsport.net/en-us/>. [Accessed: 14-Aug-2017].
- [43] "BioSig Toolbox." [Online]. Available: <http://biosig.sourceforge.net/>. [Accessed: 09-Aug-2017].
- [44] J. R. Wolpaw, N. Birbaumer, W. J. Heetderks, D. J. McFarland, P. H. Peckham, G. Schalk, E. Donchin, L. a Quatrano, C. J. Robinson, and T. M. Vaughan, "Brain-computer interface technology: a review of the first international meeting," *IEEE Trans. Rehabil. Eng.*, vol. 8, no. 2, pp. 164–173, 2000.
- [45] Y. K. Meena, H. Cecotti, K. Wong-Lin, and G. Prasad, "Towards increasing the number of commands in a hybrid brain-computer interface with combination of gaze and motor imagery," in *Proc. Annu. Int. Conf. IEEE Eng. Med. Biol. Soc., EMBS*, 2015, pp. 506–509.
- [46] M. Kuba, Z. Kubová, J. Kremláček, and J. Langrová, "Motion-onset VEPs : Characteristics , methods , and diagnostic use," *Vision Res.*, vol. 47, pp. 189–202, 2007.
- [47] M. Kuba, *Motion-onset Visual Evoked Potentials and their Diagnostic Applications*. Nucleus HK, 2006.
- [48] O. Stelt, A. Kok, F. Smulders, J. Snel, and W. Gunning, "Cerebral Event-related Potentials Associated with Selective Attention to Color : Developmental Changes from Childhood to Adulthood," *Psychophysiology*, vol. 35, no. 1, pp. 227–239, 1998.
- [49] M. W. G. Dye and D. Bavelier, "Differential development of visual attention skills in school-age children," *Vision Res.*, vol. 50, no. 1, pp. 452–459, 2010.
- [50] I. M. Ólafsdóttir, T. Kristjánsson, S. Gestsdóttir, Ó. I. Jóhannesson, and Á. Kristjánsson, "Understanding visual attention in childhood : Insights from a new visual foraging task," *Cogn. Res. Princ. Implic.*, vol. 1, no. 18, pp. 1–12, 2016.
- [51] D. Coyle, J. Garcia, A. R. Satti, and T. M. McGinnity, "EEG-based continuous control of a game using a 3 channel motor imagery BCI: BCI game," in *IEEE Symposium on Computational Intelligence*, 2011, pp. 88–94.
- [52] J. R. Wolpaw, N. Birbaumer, D. J. McFarland, G. Pfurtscheller, and T. M. Vaughan, "Brain-computer interfaces for communication and control," *Clin. Neurophysiol.*, vol. 113, no. 6, pp. 767–91, Jun. 2002.
- [53] D. Marshall, D. Coyle, S. Wilson, and M. Callaghan, "Games , Gameplay , and BCI : The State of the Art," *IEEE Trans. Comput. Intell. AI Games*, vol. 5, no. 2, pp. 82–99, 2013.
- [54] A. Nijholt, D. P.-O. Bos, and B. Reuderink, "Turning shortcomings into challenges: Brain-computer interfaces for games," *Entertain. Comput.*, vol. 1, no. 2, pp. 85–94, Apr. 2009.
- [55] B. Keros, F. Skola, and F. Liarokapis, "EEG-based BCI and video games: a progress report," *Virtual Real.*, no. 1, pp. 1–17, 2017.
- [56] J. R. Wolpaw, "Brain-computer interfaces as new brain output pathways," *J. Physiol.*, vol. 579, no. Pt 3, pp. 613–619, 2007.